

## EVIDENCE THAT THE WOLF-SPIDER *LYCOSA TARENTULA* (ARANEAE, LYCOSIDAE) NEEDS VISUAL INPUT FOR PATH INTEGRATION

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**ABSTRACT.** The homing behavior of *Lycosa tarentula* (Linnaeus 1758) (Araneae, Lycosidae) adult females was studied. They were tested under two conditions, diffused light (200 lux) and darkness, after having been placed in an open field. In both conditions the spiders did not orient towards the burrow position; instead, under diffused light, each spider turned at a constant angle with a value close to  $135^\circ$ ; this is the turn that the spider should have made in its terrarium to return to the burrow. In darkness, most of the spiders (71.4%) turned at random. In both conditions, the trajectory was roughly straight, finishing with a sudden directional change. The speed was higher under diffused light than under darkness. These results support the hypothesis that *L. tarentula* uses path integration in laboratory conditions and that it needs visual input to obtain a direction estimation in homing.

**Keywords:** Direction estimation, spiders, Lycosidae, *Lycosa tarentula*, vision

Most animals have a home range where they move about to find food or to locate mates. After these displacements, animals must be able to reach a spatially restricted area known to the animal: its shelter or home. Movements that enable the animal to find its shelter or home are known as homing. There are several homing mechanisms (Papi 1992), path integration being one of the most frequently used by arthropods. In path integration, the animal can return to some known point, for example, its burrow, without exteroceptive spatial information such as landmarks. While moving, the animal measures and integrates the angular changes in direction and distances traveled between each change of direction to obtain a vector whose orientation indicates home direction and whose length indicates home distance. The animal can use outward-journey information obtained through internal references, e.g., exoskeleton sense organs (Seyfarth et al. 1982; Mittelstaedt 1983; Görner & Claas 1985; Durier & Rivault 1999) or by use of external cues such as the sun or the celestial polarized-light pattern (Wehner 1997) to determine its homeward direction.

In both insects (desert ant, *Cataglyphis bicolor* (Fabricius 1793), Wehner & Srinivasan 1981; cockroach larvae, *Blattella germanica*

(Linnaeus 1767), Durier & Rivault 1999) and spiders (funnel web spider, *Agelena labyrinthica* (Clerck 1757), Moller & Görner 1994), the knowledge of distance, the other component of path integration, is expressed by a change of direction to begin a systematic search for the nest. During this search the animal returns several times to the same point while the radius of its displacement becomes greater each time.

It has been demonstrated in the funnel web spider, *A. labyrinthica* (Görner & Claas 1985), that there is an orientation change in the homeward run when the azimuthal position of a light present during this run is changed by  $90^\circ$ . However, the mean deviation is smaller ( $66^\circ$  at a light intensity of 800 lux and  $42^\circ$  at 22 lux) than one would expect from the angular shift of the light source. This indicates that, as would be expected given that *A. labyrinthica* is a web-building spider, it does not rely exclusively on visual stimuli. Homing has also been studied in the nocturnal ctenid spider *Cupiennius salei* (Keyserling 1877) (Seyfarth et al. 1982). In this study, after having captured prey, spiders were gently chased off following either a rectilinear trajectory or a semicircular one. Seyfarth et al. (1982) demonstrated that the animal needs proprioceptive information for homing because operated an-

imals—spiders with the lyriform slit sense organs of the femur and tibia destroyed mechanically—returned with less success to the site from which they had been chased. In *C. salei*, Schmid (1997) noted differences in locomotion depending upon whether the spiders were in bright light or complete darkness.

In the lycosid spider *Lycosa tarentula* it has been demonstrated that the spider uses the celestial polarized-light pattern for homing (Ortega-Escobar & Muñoz-Cuevas 1999) and that this information is gathered through the anterior median eyes which, according to Koivoo et al. (1993), have visual cells with orthogonally arranged rhabdoms. Spiders made an L-shaped outward path and then were moved to a featureless open field where they were placed at the center oriented at random. Sun position was masked by means of a screen. Under a clear sky, spiders oriented towards the burrow location relatively accurately, turning at a variety of angles to accomplish this; under an overcast sky, spiders oriented at random in the open field by turning an almost constant angle; when they could see a clear sky under a depolarizing sheet, they also oriented at random. Thus *L. tarentula* could not have used a landmark-based navigational strategy because, after the outward trip, they were moved to a featureless open field 2 m from their home terrarium and animals became oriented at random when there was no directional celestial information (sun azimuth or polarized-light pattern). In the same study, we observed (unpublished data) that under an overcast sky, spiders had a tendency to turn at a fixed angle relative to their starting direction in the open field, an angle which, in their terrarium, would have carried them near their burrows.

In this study, I describe the navigational strategy that *L. tarentula* uses in the absence of celestial cues in the laboratory and its dependence on visual information.

## METHODS

**Subjects.**—Thirteen adult female *L. tarentula* from our laboratory stock were used. They were maintained in individual containers measuring 17 x 13 x 8 cm and they were fed mealflies (*Calliphora vomitoria* (Linnaeus 1758)) and given water twice a week.

**Homing under lighting.**—To begin the study of homing orientation, animals were

placed in a terrarium measuring 60 x 30 x 35 cm. This terrarium had a 15 cm deep substratum of soil; in the middle of one long side of the terrarium, an artificial burrow was built, similar to that which the spider digs in the field. After 5 days of habituation to the terrarium, the experiment began. Spiders were gently pushed along the edge of the terrarium on a path traversing half the length and the full width of the terrarium (Fig. 1). When the spider arrived at the end of the path, it was placed into a transparent open glass container and transferred to the center of an open field 90 cm in diameter (wall height, 48 cm; visual angle, 47°). Both the terrarium and the open field were in a room without natural lighting. The room was lit in the daytime (0800–2000 h) with white light by two SYLVANIA Standard F36W fluorescent tubes producing 200 lux at the floor level of the open field. Each animal was observed 8 times and placed in one of the following compass directions at random: 0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°. The spider's orientation was recorded when it was at a distance of 20 cm from the center of the open field. If the spider had not moved during 20 minutes it was returned to the terrarium. The floor of the open field was thoroughly cleaned before each test.

**Automated video tracking.**—The image of the open field was captured by an Ikegami ICD-42B B/W CCD video camera and displayed on a Sony Trinitron color video monitor. Simultaneously, the video signal was digitized by a Targa + frame grabber that was interfaced with a personal computer supporting an object video-tracking system (EthoVision, Noldus Information Technology, Wageningen, The Netherlands). In this way, we obtained a time series of x,y positions that EthoVision used to build up the path followed by the spider during its locomotion. In the present study, the system was configured to sample the spider's location at 5 Hz.

The following parameters were determined: 1. topographic bearing of the homeward trip, 2. bearing relative to the initial orientation ( $\alpha$  angle), and 3. displacement speed.

**Homing in darkness.**—Eight of the thirteen animals studied under the light condition were afterwards studied in their subjective darkness. The spiders were observed under infrared light (to which the video camera was sensitive) and under a Phillips darkroom lamp

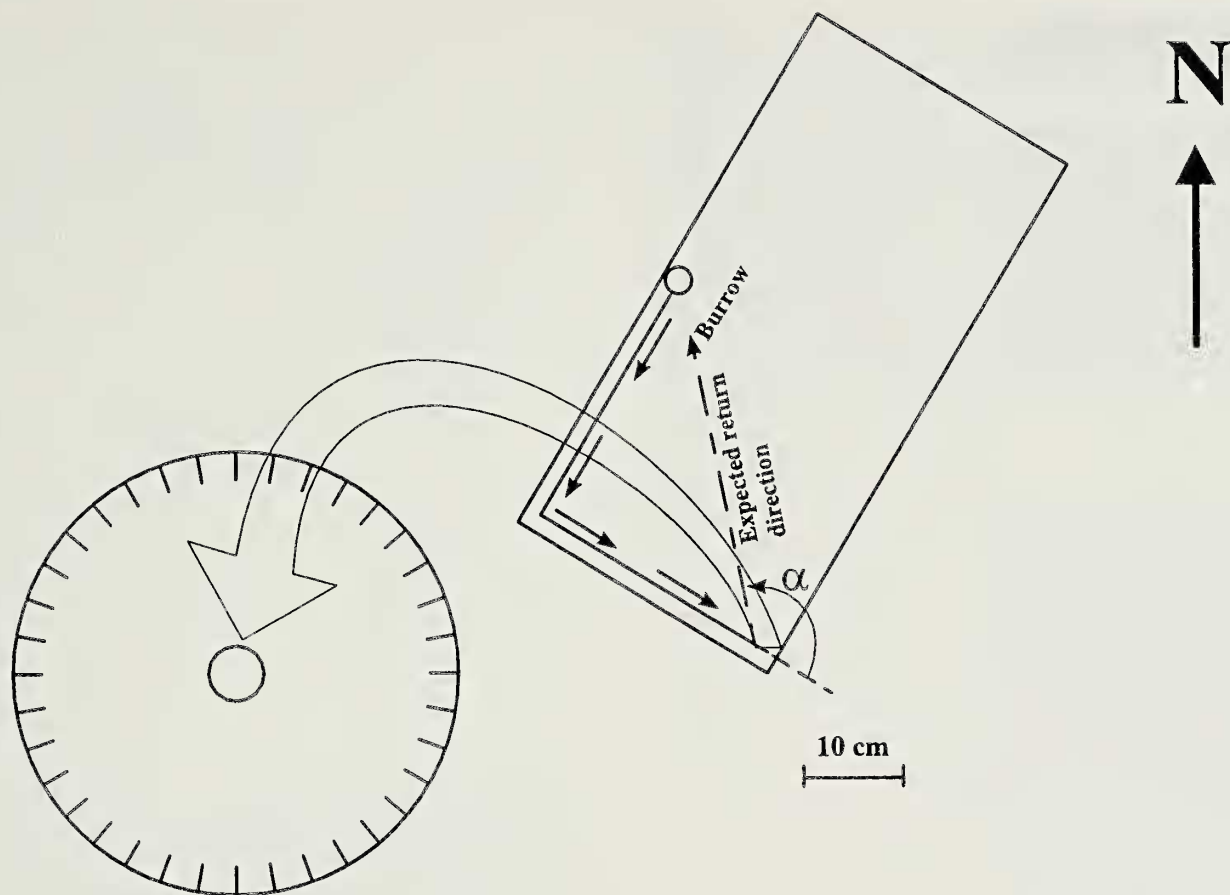


Figure 1.—Setup used to study homing in *L. tarentula*. Right, top view of terrarium in which the animal lived during the study; arrows indicate the outward path. Left, dorsal view of the open field in which the animal was left after being taken from the right corner opposite to the burrow. Burrow direction was at  $350^\circ$ . The big arrow indicates the transfer of the animal to the center of the open field (shown at half of its actual size in relation to the terrarium). To go to the burrow, the spider must turn an  $\alpha$  angle of  $135^\circ$  in its terrarium.

so that the observer could guide the spider out of the nest. To check that the spider did not see this red darkroom light, we studied the locomotor activity cycle of four animals under an LD 12:12 cycle in which the light was supplied by the Phillips darkroom lamp. Under these conditions, the spiders showed a freerunning rhythm similar to that observed under constant conditions of darkness (DD); these results indicate that the spider cannot distinguish between the light and dark conditions of the cycle (Fig. 2). Tracking of locomotor activity under subjective darkness was carried out in a similar way to that described for homing under lighting.

**Statistical analyses.**—The directions followed by the animals are shown as circular distributions, which were analyzed using circular statistics (Batschelet 1981) calculating  $\Phi$  (mean orientation angle) and  $r$  (length of the mean vector, ranging from 0–1). Significance was estimated using the Rayleigh test and 95% confidence limits. In order to make comparisons between the mean angles of several animals, we have used the non-parametrical Moore's test (Batschelet 1981). These statis-

tical tests have been fully described elsewhere (Ortega-Escobar & Muñoz-Cuevas 1999).

We tested the topographic bearings to evaluate whether there was an effect of distant visual landmarks or other cues on homing direction and, as there was not such an effect, afterwards we converted the topographic bearings into angles relative to the initial direction in the open field ( $\alpha$ ).

Comparisons among speeds were carried out by means of a two-factor ANOVA within-subjects design, one within-factor with two levels (light/darkness) and another within-factor with seven levels (subjects).

## RESULTS

**Homing under lighting.**—Paths followed by the spiders in the open field were roughly straight, finishing with a sudden turn either to the right or to the left, followed by a turn in the opposite direction (Fig. 3).

This series of turns has also been observed when the animal is taken from the burrow without having been displaced and transferred to the center of the open field. This type of

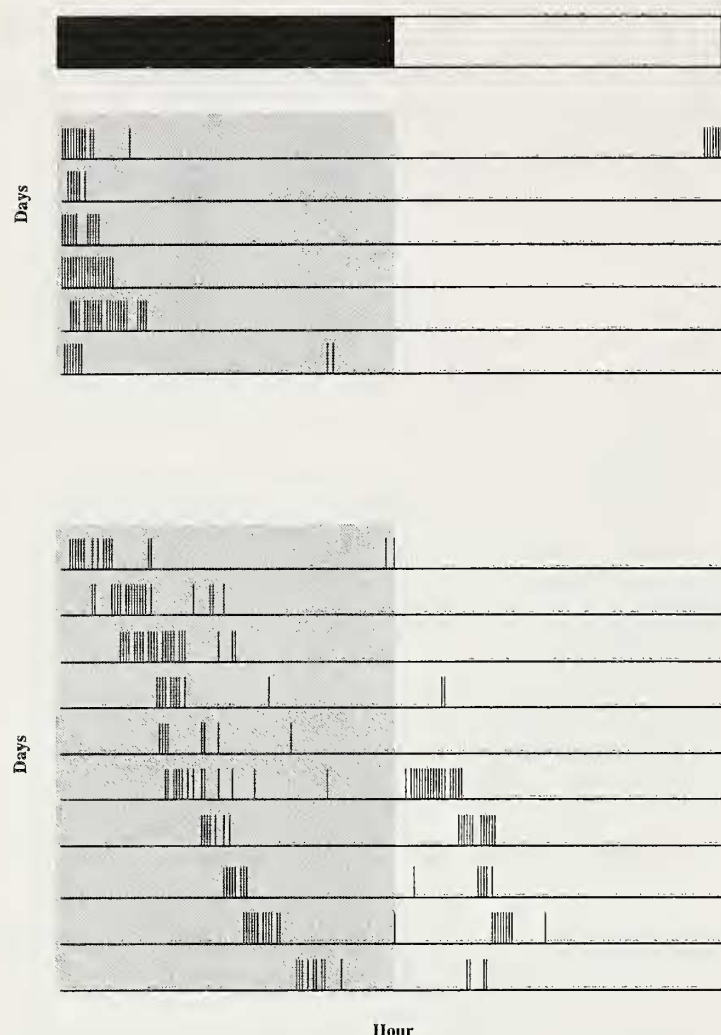


Figure 2.—Top: Locomotor activity rhythm of an animal submitted to a LD cycle 12 (white light):12 (darkness); it can be observed that the locomotor activity is adjusted to the LD cycle. Bottom: Locomotor activity rhythm of an animal submitted to a LD cycle 12 (red light):12 (darkness); it can be observed that locomotor activity is freerunning.

behavior has been called systematic search and we have not analyzed it in this study.

Some spiders defecated in the open field before homing; in order to do this they walked backwards a variable distance, generally never less than 5 cm, defecated, and then began homing. We have not used these paths in our analysis.

None of the 13 spiders used in this experiment oriented towards the burrow or towards another point of the room in a constant way in the eight tests (Fig. 4a). However,  $\alpha$  was non-randomly oriented in 12 of the 13 animals (Fig. 4b). The mean vectors of these 12 animals were not statistically different (Moore's Test:  $D = 1,512$ ,  $P < 0.05$ ).

**Homing in darkness.**—The homeward paths of these animals were very similar to those observed under lighting: they were roughly straight, finishing by systematic searching. The topographic bearings (Fig. 4c) have a random orientation except in one ani-

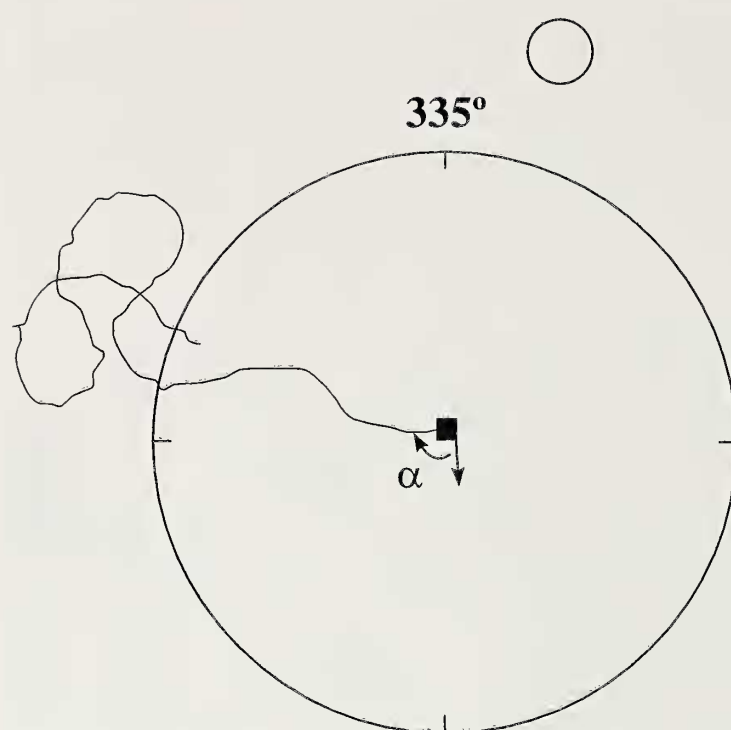


Figure 3.—Example of a homing path in the open field under lighting. The black square in the center represents the point where the spider is placed and her orientation is indicated by the arrow; the little circle represents the burrow compass direction.  $\alpha$  is the angle between the initial orientation and final bearing.

mal. The angle  $\alpha$  (Fig. 4d) has also a random orientation in five (71.4%) of the seven animals. There are only 7 vectors under the darkness condition because one of the animals did not walk in any of the 8 tests.

**Comparisons of the speed in both conditions.**—The mean velocity for all the subjects under lighting was  $2.03 \pm 0.31 \text{ cm} \cdot \text{s}^{-1}$ ; the mean value for all the subjects in darkness was  $0.93 \pm 0.10 \text{ cm} \cdot \text{s}^{-1}$ . ANOVA revealed a significant effect of lighting on the velocity along the homeward path,  $F_{(1,7)} = 10.487$ ,  $P = 0.014$ , while there were no differences between subjects,  $F_{(6,42)} = 1.313$ ,  $P = 0.273$  and the interaction of lighting condition vs. subjects was not significant,  $F_{(6,42)} = 1.654$ ,  $P = 0.156$ .

## DISCUSSION

Our results show that, during the day, *L. tarentula* does not orient towards the topographic burrow position under the experimental conditions of the absence of tacto-chemical information and the presence of distant visual landmarks of the laboratory. Inside the open field the animal could still use  $50^\circ$  of the visual field of the posterior median eyes or the posterior lateral eyes (Land 1985) to see distant visual landmarks. Nonetheless, the spider

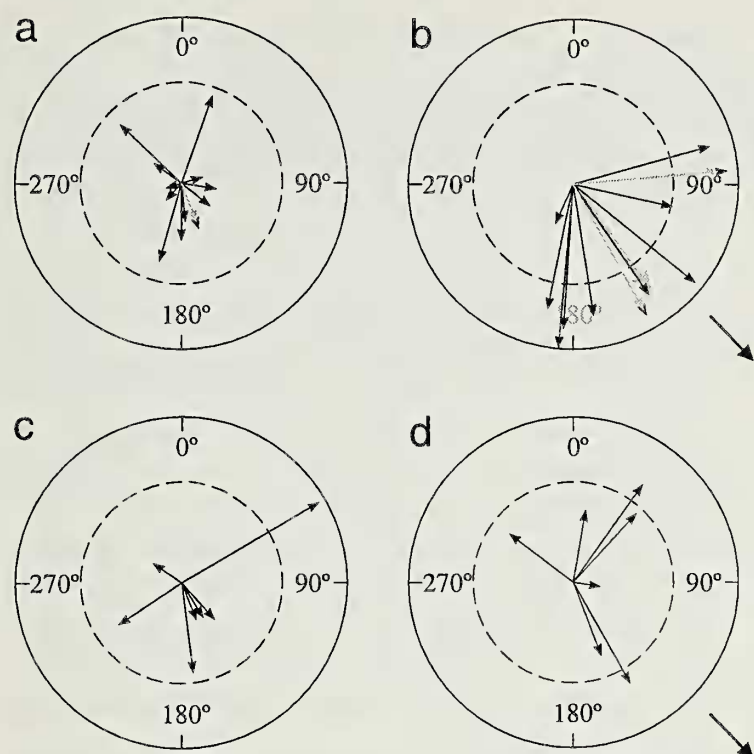


Figure 4.—a. Mean vectors of the topographic bearings of the animals studied under the light condition. Burrow direction is at 350°. The dashed circle indicates the critical  $r$ -value of  $P = 0.05$ . b. Mean vectors of  $\alpha$  (the angle of movement relative to the initial orientation in the open field) of the animals studied under the light condition. The thick gray arrow represents the mean vector of all the animals ( $\alpha = 144^\circ$ ).  $0^\circ$  indicates that the animal looks for home in the same direction as its initial orientation in the open field. The external arrow represents the angle the spider must turn to, in effect, go back to the burrow ( $\alpha = 135^\circ$ ). c. Mean vectors of the topographic bearings of the animals studied under dark condition. d. Mean vectors of  $\alpha$  of the animals studied under the dark condition.

did not orient towards its burrow. These results are in agreement with what has been observed when the animals could use neither the sun nor the polarized light pattern for homing (Ortega-Escobar & Muñoz-Cuevas 1999). In contrast, under diffuse non-polarized light, *L. tarentula* try to return home by turning a fixed angle,  $\alpha \sim 135^\circ$ . A turn of  $135^\circ$  would let the animal walk to a point near the burrow if the spider's orientation had not been changed in the open field. Although systematic observations were not made in the terrarium, some animals that showed  $\alpha \sim 135^\circ$  in the terrarium, also showed it in the open field and something similar was found for those with  $\alpha \sim 180^\circ$ .

To obtain the appropriate  $\alpha$ , spiders could use either idiothetic information, visual information or a combination of both. Idiothetic information was the same in both experi-

ments; however, during the day but in darkness, path integration fails to provide a correct estimate of  $\alpha$  (Fig. 4d). In another diurnal arthropod, the bumblebee (*Bombus impatiens* (Cresson 1863)), it has also been shown that path integration fails to provide a correct estimate of home direction when bees cannot use visual information (Chitka et al. 1999). So, it seems necessary that some kind of visual input be perceived during the outward path in order to achieve or activate path integration. In the wild and during the day, *L. tarentula* females walk out from their burrows only when there is prey or another conspecific, while in the night (natural darkness) they walk out spontaneously without the presence of prey or conspecifics. This different behavior must also be based on some differences between day and night eye states and the visual fields of the different eyes. I think that *Lycosa tarentula* activates path integration by using proprioceptive information and visual information gathered by the anterior lateral eyes (ALE) which have ventral visual fields whose images change very little when the animal walks in comparison with the images on the anterior median (AME), posterior median (PME) or posterior lateral eyes (PLE) that move quickly given their visual fields. In this way, it is easiest to make an association between the proprioceptive information and the visual information generated by the ALEs.

Our results contrast with those on *Cupiennius salei* (Seyfarth et al. 1982); in that study the animals could not use visual information because their eyes were masked, but they were capable of returning to the point from which they had been chased by using only proprioceptive information supplied by the lyriform organs. In addition, during their walks in darkness, *Cupiennius* (Schmid 1997) use exploratory movements of the first pair of legs, a kind of behavior that we have not observed in *L. tarentula*.

With our data we cannot analyze how *Lycosa tarentula* carries out distance estimation because although the distance that it should walk to the burrow was near 36 cm and the radius of the open field was 45 cm, there were many trials in which the animal walked as far as the open field wall and then followed it.

Walking speed is greater in the light than in the dark. Because there are no other differences in the linear aspect of the paths, that

difference seems to indicate again that *L. tarentula* needs some kind of visual information perceived during the outward trip to integrate the homeward one. In other walking arthropods, it has been observed that walking speed is lower when they cannot use ventral optic-flow cues (desert ant, *Cataglyphis fortis*, Ronacher & Wehner 2000). *Lycosa tarentula* could use a similar mechanism because it walks the same distance, 20 cm, at a higher speed under light, in the presence of self-induced optic flow, than in darkness, when there is not such information.

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